# Comments

## BIOMASS AND TOXICITY RESPONSES OF POISON IVY (TOXICODENDRON RADICANS) *TO ELEVATED ATMOSPHERIC CO$_2$: COMMENT*

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As the earth's environment changes with the alteration of important putative environmental drivers (e.g., CO$_2$, temperature, nitrogen deposition, biotic invasions, and the frequency and severity of extreme weather events), ecologists and environmental biologists are scrambling to predict what the world may look like under these new conditions. To accomplish this goal, these scientists often use experimental manipulations of the most likely drivers of community and ecosystem change, particularly CO$_2$, temperature, and nitrogen (e.g., Bergner et al. 2004, Mohan et al. 2006, Reich et al. 2006*a*). But are these relatively small-scale experiments enough to give us an accurate picture of the structure and function of a future world and is there a way to test their predictions?

In a six-year study on the impact of elevated CO$_2$ on the growth and toxicity of poison ivy (*Toxicodendron radicans*) at the Duke Forest FACE site in North Carolina, USA, Mohan et al. (2006) reported that mean plant biomass of poison ivy increased significantly more in elevated CO$_2$ than in ambient CO$_2$ (Fig. 1), and that this increase was far more than in other woody species. They found that elevated atmospheric CO$_2$ substantially increased poison ivy photosynthesis, water use efficiency, urushiol (the "toxic" compound found in poison ivy), growth, and population biomass. Consequently, Mohan et al. (2006) concluded that poison ivy is likely to become far more abundant (and toxic) with increasing concentrations of atmospheric CO$_2$. Lianas (woody vines), such as poison ivy, are hypothesized to benefit more from

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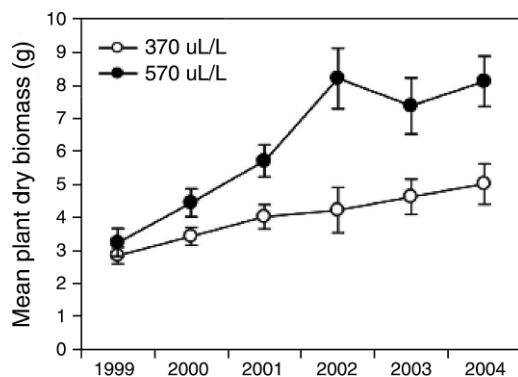[5] E-mail: Schnitze@uwm.edu

elevated CO$_2$ than other woody growth forms because lianas allocate a relatively large proportion of their biomass to leaves (a result of low structural tissue requirements), and thus they should gain more leaf area per total plant biomass with increasing CO$_2$ and carbon fixation than other growth forms. More leaf area, in turn, would allow lianas to fix even more carbon and thus increase faster in total biomass (size and abundance) with elevated CO$_2$ (e.g., Körner 2006, Mohan et al. 2006, Zotz et al. 2006). The study by Mohan and colleagues was methodologically sound and their findings and conclusions were consistent with other experimental studies on the effects of elevated CO$_2$ on liana performance (e.g., Sasek and Strain 1990, 1991, Condon et al. 1992, Granados and Körner 2002, Hättenschwiler and Körner 2003, Zotz et al. 2006). In most cases, however, we have little or no ability to test the validity of predictions based on these types of studies because we lack long-term data on the change in natural plant communities.

In a separate study, Londré and Schnitzer (2006) used empirical observations of temperate liana abundance in the interiors of 14 forests in southern Wisconsin, USA, over a 45-year period (1959–2005) to test whether these long-term data were consistent with the hypothesis that lianas, including poison ivy, have proliferated more than co-occurring trees with global change, which includes the increases in CO$_2$ (reviewed by Schnitzer and Bongers 2002, Körner 2006). Globally, atmospheric CO$_2$ levels have risen ~40% over the last 150 years, with nearly 60% of this increase occurring after 1958 (Keeling and Whorf 2005). Thus, if the predictions of experimental studies previously cited are accurate and broadly applicable, both poison ivy and total liana density and biomass should have increased in Wisconsin forests over the past 45 years.

Curiously, the empirical observations of Londré and Schnitzer did not match the predictions of experimental studies. Not only did mean liana abundance and basal area remain constant over the past 45 years in Wisconsin forests (Londré and Schnitzer 2006), but poison ivy was the only liana species to decrease significantly over this period (Fig. 2). In a separate study in an old-growth maritime forest on Fire Island in New York, USA, Forrester et al. (2006) reported that over a 19-year period (1967–1986) poison ivy ground cover decreased from nearly 10% to <1%. There are a number of potential and non-mutually exclusive explanations to reconcile the disparate findings between the predictions generated from experimental studies and the long-term observational studies.

One likely explanation is that plant growth and proliferation rates are controlled by multiple factors, not just by CO$_2$ (e.g., Körner 2006, Reich et al. 2006*b*). For example, although both mean and low winter

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FIG. 1. The change in plant biomass (mean ± SE) from 1999 until 2004 for poison ivy grown in ambient (~370 μL/L) and high (570 μL/L) $CO_2$ levels at the Duke Face site, North Carolina, USA. This figure is adapted from Mohan et al. (2006) with permission from PNAS (copyright © National Academy of Sciences, USA).

temperatures have increased in Wisconsin forests over the last 45 years (Londré and Schnitzer 2006), lianas may still be limited more by freezing winter temperatures and a short growing season than by $CO_2$. Large vessel elements and relatively thin stems that lack insulation make lianas vulnerable to freezing-induced embolism or possibly the rupturing of vessel elements, which render the vascular system inoperable and ultimately kill the plant (Sperry et al. 1987, Ewers et al. 1991). While many temperate liana species have special adaptations to avoid freezing (Sperry et al. 1987, Schnitzer 2005), these adaptations come at a cost, which includes an abbreviated growing season compared to many shrubs and trees. For example, many liana species in temperate forests flush their leaves relatively late in the spring and/or drop their leaves early in the autumn, presumably due to their vulnerability to freezing (Schnitzer 2005). Leaves of poison ivy (*T. radicans*), grape (*Vitis* spp.), and Virginia creeper (*Pathenocissus quinquefolia*) typically senesce much earlier than their host trees, resulting in a relatively short growing season (Stiles 1982). Although Stiles (1982) provided compelling evidence that early senescence by the lianas *T. radicans* and *Parthenocissus* spp. is an adaptation for seed dispersal (foliar fruit flag hypothesis), early senescence may actually be driven by the vulnerability of lianas to freezing and their need to prepare for winter (e.g., drain their vessel elements in the case of members of the Vitaceae; Schnitzer 2005).

The effect of a shorter growing season may be more detrimental for lianas in northern deciduous forests than in coniferous forests located in a moderate climate, such as the forest at the Duke FACE site. In northern deciduous forests, lianas are unable to take advantage of elevated light regimes in the early or late seasons, before overstory leaf flush and after leaf senescence, whereas competing shrubs and understory trees appear to benefit from early spring and late fall photosynthesis (Harring-

ton et al. 1989). Consequently, if an abbreviated growing season and freezing winters limit lianas, but not competing trees and shrubs, in northern deciduous forests, then the potential increases from elevated $CO_2$ may have little relative benefit to lianas in those forests compared to the pine forest at the Duke FACE site.

Light availability may also be an important determinant of liana distribution within temperate forests (Londré and Schnitzer 2006), and the interaction between elevated $CO_2$ and light availability may provide an explanation for the discrepancy between the experimental and observational studies. For instance, Hättenschwiler and Körner (2000) reported that light availability in the understory of a mixed broadleaf–coniferous forest in Switzerland strongly determined whether tree seedlings responded to elevated $CO_2$, with the growth rate of moderately shade-tolerant tree species increasing with elevated $CO_2$ only under relatively high (4.8% full sun) understory light levels; whereas, deeply shade-tolerant species responded to elevated $CO_2$ at low understory light levels (0.8% full sun; see also Zotz et al. 2006). Other studies demonstrate that the ability to use enhanced resources other than light is severely constrained in relatively shaded understories (e.g., Walters and Reich 2000). At the Duke FACE site, where Mohan et al. (2006)
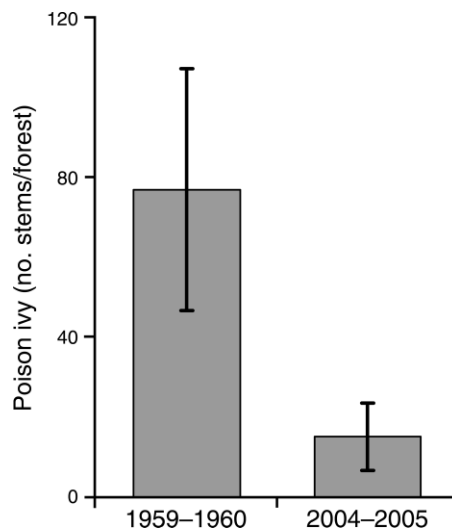


FIG. 2. The number of poison ivy vines per forest base (mean ± SE) for 14 deciduous forests in Wisconsin, USA. Lianas were censused in 1959–1960 and in 2004–2005 using 40 point quarter points (160 total measurements). Poison ivy decreased significantly over the 45-year period (Wilcoxon's signed-ranks test, $P = 0.02$, $T_S = 19.5$, df = 13). Nearly identical results were found using 40 1-$m^2$ ground cover plots in these same forests, which generally included smaller poison ivy individuals than in the point quarter method ($P = 0.01$, $T_S = 32.5$, df = 13; data from Londré and Schnitzer [2006]). Forest size was variable, but all forests were >18 ha in area and had little or no disturbance since the 1960 measurements. Because this is a relative comparison using the same methods in each forest, the actual size of each forest is not as relevant as the comparison between 1960 and 2005.

studied poison ivy, the canopy is dominated by densely planted ~25-year-old shade-intolerant loblolly pines, which, along with a mix of subcanopy hardwood trees, considerably reduce the mean understory light levels to <3% of full sunlight (J. Mohan, *personal communication*). Nevertheless, this coniferous forest may still allow more light penetration into the understory than in the older and relatively dark broadleaf deciduous forests studied by Londré and Schnitzer, which were dominated by mid- and deeply shade-tolerant species (Reich et al. 2003). A light × $CO_2$ interaction may have enhanced the response of poison ivy in the pine-dominated stand, but light may have been too limiting for $CO_2$ to have a strong effect in the shadier broadleaf stand.

The decrease in the abundance and basal area of poison ivy in Wisconsin forests over the past 45 years may be a result of natural successional changes in temperate forests, as these forests grow older and darker. If so, the successional changes in Wisconsin forests may have overwhelmed or prevented the potential increase in poison ivy abundance and biomass from increased $CO_2$. We note, however, that we lack the data necessary to test whether the understory of these forests has changed over the last half century.

A second possible explanation for the disparate findings between the experimental and observational studies is that top-down trophic control from white-tailed deer and other animals may have overwhelmed the positive effects of $CO_2$, thereby reducing poison ivy abundance over the past 45 years. Mammals were excluded from the DUKE face study so that the impact of $CO_2$ on plant growth would not be confounded by herbivory. Deer foraging, however, can substantially alter the structure and composition of temperate forests (Rooney and Waller 2003), and deer populations in southern Wisconsin have increased two- to fivefold over the past 40 years, from 52 to 129 deer/$km^2$ in the late 1960s to ~259 deer/$km^2$ in 2004 (WDNR 2004). Poison ivy is a preferred browse species for deer and other animals (Sotala and Kirkpatrick 1973), and thus the large increase in deer abundance over the last 40 years may also account for the decrease in poison ivy in Wisconsin forests. Nevertheless, excluding deer for 16 years on Fire Island (from 1986 to 2002) did not significantly increase poison ivy abundance (mean cover increased from 0.1% to just 0.4% over this period; Forrester et al. 2006), suggesting that deer are not the only factor controlling poison ivy.

A third possible explanation is that the level of $CO_2$ in the atmosphere is not yet high enough to trigger the increase in liana abundance and basal area. These increases may still be years away. While there is evidence that many species have already responded to environmental changes (e.g., many thousands of species' distributions have shifted poleward or to higher elevation; Parmesan 2006), it is possible that levels of $CO_2$ will have to be far higher than 380 ppm to allow liana species to overcome such limiting or co-limiting factors as cold winter temperature, length of growing season, light, nutrients, or top-down regulation by mammals. This claim, however, is inconsistent with the findings of Granados and Körner (2002), who reported that lianas grew 48% more at an elevated atmospheric $CO_2$ level of 420 ppm compared to 280 ppm, but that the rate of liana biomass increase dropped to 23% at 560 ppm $CO_2$ (compared to 420 ppm; see also Körner 2004). Furthermore, from a strictly physiological perspective, the effect of increasing $CO_2$ on plant growth rate may be relatively small compared to the effects of natural microhabitat variability in light or soil nutrients. The latter can lead to 100-fold (or greater) differences in growth of individual plants, whereas a small increase in $CO_2$ resulted in ~50% increase in liana biomass (Granados and Körner 2002), and more generally, a doubling of $CO_2$ typically results in a ~1.3-fold increase in plant growth on average (Ainsworth and Long 2005). Thus, variability of resources could mask, limit, or even eliminate the $CO_2$ effect for poison ivy in many habitats.

A fourth potential explanation may be the artificial nature of elevated $CO_2$ studies themselves. Klironomos et al. (2005) reported that communities and ecosystems respond very differently to the large, single-step increases in $CO_2$ implemented by most studies, compared with the more gradual increases in $CO_2$ that are occurring in the atmosphere. This finding may be due to the ability of plants to acclimate physiologically to gradual increases in $CO_2$ via plastic responses or microevolutionary changes (e.g., Ward and Kelly 2004, Körner et al. 2005), which would be less likely with a large, single-step increase. If this scenario is true, the lack of change in liana abundance or basal area in Wisconsin forests over the last 45 years may be attributable to the gradual physiological acclimation of plant populations to the increase in atmospheric $CO_2$, without a net change in the competitive hierarchy among growth forms.

Long-term observational studies, such as that of Londré and Schnitzer (2006), provide information on how communities and ecosystems are changing over time; however, they provide little capacity to explain the mechanisms responsible for that change (or lack thereof). In contrast, controlled experimental studies, such as that of Mohan et al. (2006), can precisely examine the putative factors controlling plant communities. Elevated atmospheric $CO_2$ may indeed increase poison ivy abundance and biomass in forests, as predicted by Mohan and colleagues, but this increase may become evident only when other overriding factors are removed. Consequently, extrapolating the findings of single-factor experimental studies to predict future community and ecosystem level changes remains exceedingly difficult, and we have yet to determine how broadly to apply predictions from these experiments. While the extent to which the findings of relatively small-scale experimental studies are universal is a

common dilemma in ecology, predictions generated from studies on global environmental change differ in that they typically cannot be tested without long-term data, which often do not exist. Furthermore, because we typically test only one to a few factors of environmental change (e.g., $CO_2$, N, ozone), we are unable to make accurate predictions beyond those particular factors.

Although far from perfect, controlled global change studies such as those of Mohan and colleagues likely still provide the best available insight for predicting the nature, direction, and magnitude of global change on community dynamics and ecosystem function in a future environment. Factorial approaches that manipulate multiple putative factors that control plant dynamics may further elucidate the relative importance of and interactions among these factors. Nevertheless, the differing results between the experimental and observational studies mentioned here illustrate the difficulty in predicting large-scale, long-term effects from relatively small-scale experimental studies. Long-term observational studies can serve as a guide for controlled experiments, while controlled experiments can serve to test possible mechanisms involved in long-term observed trends, and both approaches combined will provide more accurate predictions of community composition, dynamics, and ecosystem function in a future environment than will either approach alone.

*Literature cited*

Ainsworth, E. A., and S. P. Long. 2005. What have we learned from 15 years of free-air $CO_2$ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising $CO_2$. New Phytologist 165:351–372.

Bergner, B., J. Johnstone, and K. Treseder. 2004. Experimental warming and burn severity alter soil $CO_2$ flux and soil functional groups in a recently burned boreal forest. Global Change Biology 10:1996–2004.

Condon, M. A., T. W. Sasek, and B. R. Strain. 1992. Allocation patterns in two tropical vines in response to elevated atmospheric $CO_2$. Functional Ecology 6:680–685.

Ewers, F. W., J. B. Fisher, and K. Fichtner. 1991. Water flux and xylem structure in vines. Pages 127–160 *in* F. E. Putz and H. A. Mooney, editors. The biology of vines. Cambridge University Press, Cambridge, UK.

Forrester, J. A., D. J. Leopold, and H. B. Underwood. 2006. Isolating the effects of white-tailed deer on the vegetation dynamics of a rare maritime American holly forest. American Midland Naturalist 156:135–150.

Granados, J., and C. Körner. 2002. In deep shade, elevated $CO_2$ increases the vigor of tropical climbing plants. Global Change Biology 8:1109–1117.

Harrington, R. A., B. J. Brown, and P. B. Reich. 1989. Ecophysiology of exotic and native shrubs in southern Wisconsin: I. Relationship of leaf characteristics, resource availability, and phenology to seasonal patterns of carbon gain. Oecologia 80:356–367.

Hättenschwiler, S., and C. Körner. 2000. Tree seedling responses to *in situ* $CO_2$-enrichment differ among species and depend on understorey light availability. Global Change Biology 6:213–226.

Hättenschwiler, S., and C. Körner. 2003. Does elevated $CO_2$ facilitate naturalization of the non-indigenous *Prunus laurocerasus* in Swiss temperate forests? Functional Ecology 17:778–785.

Keeling, C. D., and T. P. Whorf. 2005. Atmospheric $CO_2$ records from sites in the SIO air sampling network. *In* Trends: a compendium of data on global change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, USA.

Klironomos, J. N., M. F. Allen, M. C. Rillig, J. Pietrowski, S. Makvandi-Nejad, B. E. Wolfe, and J. R. Powell. 2005. Abrupt rise in atmospheric $CO_2$ overestimates community response in a model plant–soil system. Nature 433:621–624.

Körner, C. 2004. Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. Philosophical Transactions of the Royal Society B 359:493–498.

Körner, C. 2006. Forests, biodiversity and $CO_2$: surprises are certain. Biologist 53:82–90.

Körner, C., R. Asshoff, O. Bignucolo, S. Hättenschwiler, S. G. Keel, S. Pelaz-Riedl, S. Pepin, R. T. W. Siegwolf, and G. Zotz. 2005. Carbon flux and growth in mature deciduous forest trees exposed to elevated $CO_2$. Science 309:1360–1362.

Londré, R. A., and S. A. Schnitzer. 2006. The distribution of lianas and their change in abundance in temperate forests over the past 45 years. Ecology 87:2973–2978.

Mohan, J. E., L. H. Ziska, W. H. Schlesinger, R. B. Thomas, R. C. Sicher, K. George, and J. S. Clark. 2006. Biomass and toxicity responses of poison ivy (*Toxicodendron radicans*) to elevated atmospheric $CO_2$. Proceedings of the National Academy of Sciences (USA) 103:9086–9089.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

Reich, P. B., S. E. Hobbie, T. Lee, D. S. Ellsworth, J. B. West, D. Tilman, J. M. H. Knops, S. Naeem, and J. Trost. 2006*a*. Nitrogen limitation constrains sustainability of ecosystem response to $CO_2$. Nature 440:922–925.

Reich, P. B., B. A. Hungate, and Y. Luo. 2006*b*. Carbon–nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. Annual Reviews in Ecology and Systematics 37:611–636.

Reich, P. B., I. Wright, J. Cavender-Bares, J. M. Craine, J. Oleksyn, M. Westoby, and M. B. Walters. 2003. The evolution of plant functional variation: traits, spectra and strategies. International Journal of Plant Sciences 164(Supplement):S143–S164.

Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management 181:165–176.

Sasek, T. W., and B. R. Strain. 1990. Implications of atmospheric $CO_2$ enrichment and climatic change for the distribution of two introduced vines in the U.S.A. Climatic Change 16:31–51.

Sasek, T. W., and B. R. Strain. 1991. Effects of carbon dioxide enrichment on the growth and morphology of an introduced and a native honeysuckle vine species. American Journal of Botany 78:69–75.

Schnitzer, S. A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. American Naturalist 166:262–276.

Schnitzer, S. A., and F. Bongers. 2002. The ecology of lianas and their role in forests. Trends in Ecology and Evolution 17:223–230.

Sotala, D. J., and C. M. Kirkpatrick. 1973. Foods of white-tailed deer, *Odocoileus virginianus*, in Martin County, Indiana. American Midland Naturalist 89:281–286.

Sperry, J. S., N. M. Holbrook, M. H. Zimmerman, and M. T. Tyree. 1987. Spring filling of xylem vessels in wild grapevine. Plant Physiology 83:414–417.

Stiles, E. W. 1982. Fruit flags: two hypotheses. American Naturalist 120:500–509.

Walters, M. B., and P. B. Reich. 2000. Seed size, nitrogen supply and growth rate affect tree seedling survival in deep shade. Ecology 81:1887–1901.

Ward, J. K., and J. Kelly. 2004. Scaling up evolutionary responses to elevated $CO_2$: lessons from Arabidopsis. Ecology Letters 7:427–440.

WDNR (Wisconsin Department of Natural Resources). 2004. Southern forest communities. Ecological landscapes of Wisconsin—Ecosystem Management Planning Handbook, HB1805.1. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.

Zotz, G., N. Cueni, and C. Körner. 2006. *In situ* growth stimulation of a temperate zone liana (*Hedera helix*) in elevated $CO_2$. Functional Ecology 20:763–769.

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# BIOMASS AND TOXICITY RESPONSES OF POISON IVY (TOXICODENDRON RADICANS) *TO ELEVATED ATMOSPHERIC CO2: REPLY*

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Schnitzer et al. (2008) contrast results from a recent experimental study documenting increased growth of poison ivy (*Toxicodendron radicans*) in the free-air carbon dioxide enrichment (FACE) facility in the Duke Forest, North Carolina (Mohan et al. 2006), to an uncontrolled observational study finding decreased abundance of poison ivy in Wisconsin forests between 1959 and 2005 (Londré and Schnitzer 2006). Schnitzer et al. (2008) accurately point out that controlled field studies may not always emulate long-term responses in uncontrolled "real world" forests. The lack-of-change in overall vine abundance in the Wisconsin forests is in contrast to previous studies showing recent increases in the abundance of vines in temperate (Myster and Pickett 1992, Dillenburg et al. 1995, Allen 2007, Allen et al. 2007) and tropical forests (Laurance et al. 2001, Phillips et al. 2002, 2005, Wright et al. 2004), as well as our Duke FACE poison ivy study that suggests increases in vine growth at elevated atmospheric $CO_2$. Data from the Duke experiment highlight the impact of deer and rabbit herbivory for understory plants, and a recent deer-exclosure study (Forrester et al. 2006) cited by Schnitzer et al. (2008) suggests that the difference between our studies may stem from mammalian herbivory on poison ivy. We additionally address the idea that understory light limitation may explain the differential responses of poison ivy in the two studies.

Londré and Schnitzer (2006) compare abundances of woody vines (lianas), including poison ivy, in 14 southern Wisconsin forests in 2005 with abundances previously recorded in 1959. The authors found that the overall abundance of vines was not different between the two years, and that poison ivy was actually less abundant in 2005 than it was in 1959. Schnitzer et al. (2008) point out that any observed differences between these two years could be due to many potential causes, such as successional development, degree of fragmentation, increasing temperatures, rising atmospheric $CO_2$, or increasing deer populations, as well as land use histories, nitrogen deposition, increasing atmospheric ozone, and other changes over time including a host of unknown variables.

Schnitzer et al. (2008) present several mechanisms to potentially reconcile differences in the results from the Duke FACE experiment with their observations in the Wisconsin forests, including deer herbivory and light limitation. We believe mammalian herbivory is largely responsible for the different responses of poison ivy in the two studies, as the Duke poison ivy plants were protected from deer and rabbits while the Wisconsin plants were not. The negative impacts of overly abundant mammalian herbivores on forest understory plants are well known (Leopold et al. 1947, Alverson et al. 1988, DeSteven 1991, Alverson and Waller 1997, Augustine and Jordan 1998, Opperman and Merenlender 2000, Terborgh et al. 2001). As Schnitzer et al.
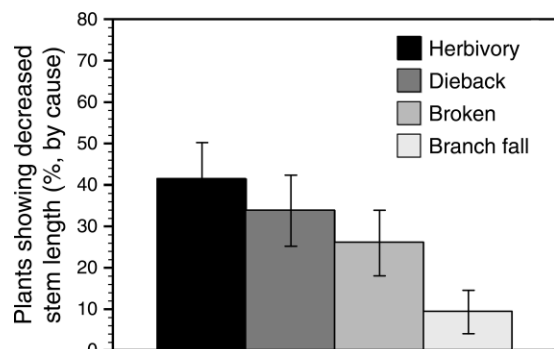
FIG. 1. Causes of decreased stem lengths (heights) between autumn 1996 and spring 1997 (the initiation of the Duke FACE experiment) in the FACE forest understory. Bars represent percentages (mean ± SE) of "shrunken plants" (understory trees, shrubs, and vines) that exhibited symptoms of mammalian herbivory, stem dieback, broken stems, or stems snapped by fallen canopy tree branches. When only poison ivy stems were analyzed, the percentage of stems preyed upon by mammals increased to 88%. Mammalian herbivory data presented here may be biased toward rabbit herbivory; rabbits possess both upper and lower incisors and cut stems at a 45° angle, leaving very distinctive bite signatures. Deer lack upper incisors and tear or rip plant stems; deer herbivory can be difficult to distinguish from other causes of stem breakage, so the "broken" data likely include stems that were eaten by deer. "Dieback" represents stems with the terminal portion still present but dead and is often a sign of fungal (or other) pathogens or drought stress.

(2008) report, a two- to fivefold increase in Wisconsin deer populations has occurred over the last 40 years, and the deer population in North Carolina tripled between 1983 and 1998 (data *available online*),[10] particularly in forests like the Duke FACE, which are adjacent to urban and suburban development (information *available online*).[11] Poison ivy is a favorite forage crop of many wildlife species including white-tailed deer and rabbits (Gillis 1971, Hoppes 1988, Penner et al. 1999, Suthers et al. 2000). Forrester et al. (2006) found that poison ivy abundance increased fourfold after 16 years of deer exclusion (due to the small sample size, none of the plant species in this study exhibited statistically significant responses to deer exclusion), and poison ivy was one of only three species whose abundance declined significantly in response to increasing deer populations before the exclosure study began. Similarly, recent work in two temperate South Carolina forests, where habitat change and human hunting has maintained stable or even declining deer populations since the mid-1990s (data *available online*),[12] documents increased density and

growth of poison ivy during the last 12–22 years (Allen 2007, Allen et al. 2007).

At the Duke FACE experiment we are finding that mammalian herbivores mediate some plant responses to atmospheric $CO_2$ (Figs. 1 and 2). Poison ivy plants accessible to deer and rabbits show no statistically significant effect of $CO_2$ on survivorship. However, these unprotected plants exhibit much higher mortality rates than their herbivore-protected (caged) counterparts (Fig. 2). The high mortality rates of poison ivy plants available to herbivores, and the potential for such plants growing at elevated $CO_2$ to have higher mortality than ambient-grown plants, may help explain the declining poison ivy cover in Wisconsin forests.

Schnitzer et al. (2008) also reason that the understory of the older Wisconsin forests may offer a lower light environment than the Duke Forest, and that greater light limitation may have increased the mortality of poison ivy plants and reduced their abundance in the northern forests. Schnitzer et al. present no data for light intensities in the Wisconsin forests, but understory light levels at the loblolly pine plantation at FACE, often <2–3% full sunlight (Mohan et al. 2007), are unlikely to be substantially different from the Wisconsin stands.

The works of Londré and Schnitzer (2006) and Schnitzer et al. (2008) highlight the limitations of both controlled experiments and purely observational studies,
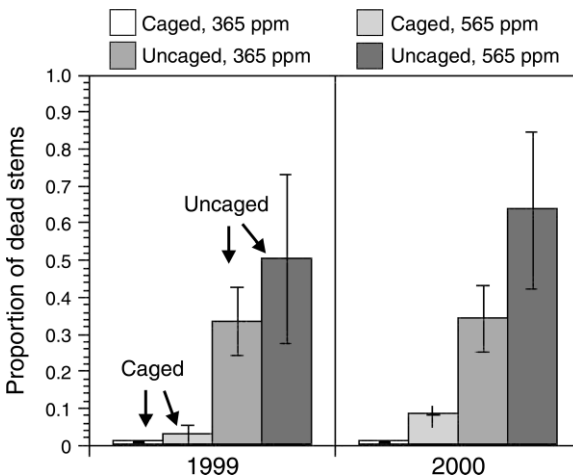


FIG. 2. Cumulative mortality (mean ± SE) of poison ivy stems (ramets) growing in the Duke Forest FACE experiment (*n* = 3 plots/treatment). "Caged" plants (paler gray) are plants protected from mammalian herbivores; "uncaged" plants are available to both deer and rabbit herbivores. Note the high mortality of uncaged plants at both $CO_2$ concentrations. Whether or not a plant was accessible by herbivores highly influenced its mortality probability ($P < 0.0001$). Although there is no significant $CO_2$ effect on mortality, there is an important $CO_2 \times$ cage interaction ($P = 0.026$), suggesting that the effects of herbivores on poison ivy mortality is influenced by atmospheric $CO_2$ concentrations. Caged plants growing at ambient $CO_2$ had 0% mortality in years 1999 and 2000.

and the value of long-term ecological data. Clearly, uncontrolled observational studies can reveal important changes in ecosystem structure over time and may suggest potential reasons for differential behavior of natural ecosystems, but controlled experiments are required to determine the underlying, mechanistic reasons for change. By combining the observational work in Wisconsin and the controlled $CO_2$ and herbivory experiments at Duke, we gain insights regarding the importance of top-down control for structuring ecological systems in an increasing-$CO_2$ world.

*Literature cited*

Allen, B. P. 2007. Vegetation dynamics and response to disturbance in floodplain forest ecosystems with a focus on lianas. Dissertation. Ohio State University, Columbus, Ohio, USA.

Allen, B. P., R. R. Sharitz, and P. C. Goebel. 2007. Are lianas increasing in importance in temperate floodplain forests in the southeastern United States? Forest Ecology and Management 242:17–23.

Alverson, W. S., and D. M. Waller. 1997. Deer populations and the widespread failure of hemlock regeneration in northern forests. Pages 280–297 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.

Alverson, W. S., D. M. Waller, and S. L. Solheim. 1988. Forests too deer: edge effects in northern Wisconsin. Conservation Biology 2:348–358.

Augustine, D. J., and P. A. Jordan. 1998. Predictors of white-tailed deer grazing intensity in fragmented deciduous forests. Journal of Wildlife Management 62:1076–1085.

DeSteven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. Ecology 72:1076–1088.

Dillenburg, L. R., A. H. Teramura, I. N. Forseth, and D. F. Whigham. 1995. Photosynthetic and biomass allocation responses of *Liquidambar styraciflua* (Hamamelidaceae) to vine competition. American Journal of Botany 82:454–461.

Forrester, J. A., D. J. Leopold, and H. B. Undersood. 2006. Isolating the effects of white-tailed deer on the vegetation dynamics of a rare maritime American holly forest. American Midland Naturalist 156:135–150.

Gillis, W. T. 1971. The systematics and ecology of poison-ivy and the poison-oaks (*Toxicodendron*, Anacardiaceae). Rhodora 73:72–152, 161–237, 370–443, 465–540.

Hoppes, W. G. 1988. Seedfall pattern of several species of bird-dispersed plants in an Illinois (USA) woodland. Ecology 69:320–329.

Laurance, W. F., D. Pérez-Salicrup, P. Delamônica, P. M. Fearnside, S. D'Angelico, A. Jerozolinski, L. Phol, and T. E. Lovejoy. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82:105–116.

Leopold, A., L. K. Sowls, and D. L. Spencer. 1947. A survey of over-populated deer ranges in the United States. Journal of Wildlife Management 11:162–177.

Londré, R. A., and S. A. Schnitzer. 2006. The distribution of lianas and their change in abundance in temperate forests over the past 45 years. Ecology 87:2973–2978.

Mohan, J. E., J. S. Clark, and W. H. Schlesinger. 2007. Long-term $CO_2$ enrichment of a forest ecosystem: implications for forest regeneration and succession. Ecological Applications 17:1198–1212.

Mohan, J. E., L. H. Ziska, W. H. Schlesinger, R. B. Thomas, R. C. Sicher, K. George, and J. S. Clark. 2006. Biomass and toxicity responses of poison ivy (*Toxicodendron radicans*) to elevated atmospheric $CO_2$. Proceedings of the National Academy of Sciences (USA) 103:9086–9089.

Myster, R. W., and S. T. A. Pickett. 1992. Dynamics of associations between plants in ten old fields during 31 years of succession. Journal of Ecology 80:291–302.

Opperman, J. J., and A. M. Merenlender. 2000. Deer herbivory as an ecological constraint to restoration of degraded riparian corridors. Restoration Ecology 8:41–47.

Penner, R., G. E. Moodie, and R. J. Staniforth. 1999. The dispersal of fruits and seeds of poison ivy, *Toxicodendron radicans*, by ruffed grouse, *Bonasa umbellus*, and squirrels, *Tamiasciurus hudsonicus* and *Sciurus carolinensis*. Canadian Field Naturalists 113:616–620.

Phillips, O. L., et al. 2002. Increasing dominance of large lianas in Amazonian forests. Nature 418:770–774.

Phillips, O. L., R. Vásquea Martínez, A. Monteagudo Mendoza, T. R. Baker, and P. Núñez. 2005. Large lianas as hyperdynamic elements of the tropical forest canopy. Ecology 86:1250–1258.

Schnitzer, S. A., R. A. Londré, J. Klironomos, and P. B. Reich. 2008. Biomass and toxicity responses of poison ivy (*Toxicodendron radicans*) to elevated atmospheric $CO_2$: Comment. Ecology 89:581–585.

Suthers, H. B., J. M. Bickal, and P. G. Rodewald. 2000. Use of successional habitat and fruit resources by songbirds during autumn migration in central New Jersey. Wilson Bulletin 112:249–260.

Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923–1926.

Wright, S. J., O. Calderon, A. Hernandez, and S. Paton. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. Ecology 85:484–489.